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No. 29: FLUCTUATIONS IN ANIMAL POPULATIONS WITH SPECIAL REFERENCE TO THOSE OF CANADA

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Fluctuations in Animal Populations with Special Reference to Those of Canada

By J. R. DYMOND, F.R.S.C.

WHILE the populations of many animals appear to remain relatively uniform over considerable periods of time, wide fluctuations characterize the populations of many others and in no country are such fluctuations more marked than in Canada.

The varying hare *(Lepus americanus)* has become an almost classic example of a species with a violently fluctuating population (Fig. 2). MacLulich (1937) estimated that in some habitats hares decreased from over three thousand per square mile to near zero in less than one year. Return to abundance in the case of the hare takes place much more slowly than does the decrease but violent fluctuations in this species have occurred at remarkably regular intervals for as long as our records extend in the past.

Another classic Canadian example of a widely fluctuating population is that of the sockeye salmon in the Fraser River. Before the curtailment of its reproduction through the partial blocking of the river by a

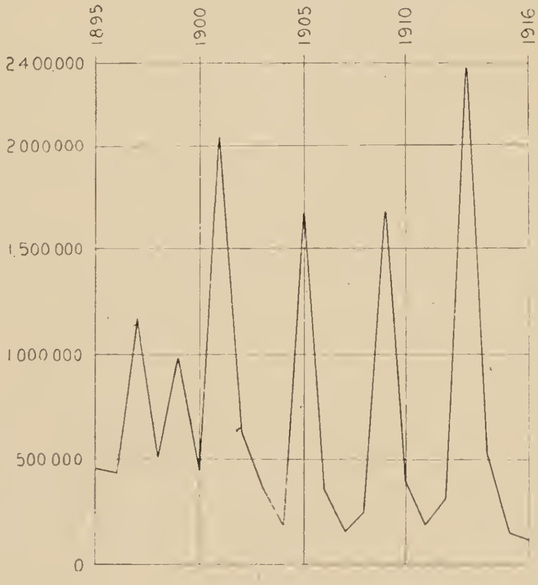

FIGURE 1.—Periodic fluctuation in abundance of Fraser River sockeye salmon, as represented by cases of canned salmon packed each year, 1895-1916 (British Columbia, Report of the Fisheries Department for 1944).

rock slide at Hell's Gate Canyon in 1913 the population as measured by the number of cases of canned fish had fluctuated between a high of nearly 2,400,000 in 1913 to a low of scarcely more than 150,000 in 1907, a variation of more than fifteen fold. In one year the population was sometimes more than eight times as large as in the preceding year.

When the Biological Board of Canada undertook in 1925 to compare artificial with natural propagation in the case of the sockeye salmon it was necessary to determine the actual number of fish entering the experimental area. This was done by building a fence across the Vedder River to stop all fish on their upward migration and constructing traps in which to catch them. By this means it was found that when populations were accurately determined the variations were actually greater than those suggested by the commercial catch. In one year (1927) 82,425 adult sockeye entered the Vedder River whereas in another (1932) only 2,259 appeared (Foerster, 1938). In this case the big run was more than thirty-six times as large as the small one.

Such fluctuations in populations, it is admitted, are exceptional. Usually animals maintain more uniform numbers from year to year but accumulating evidence suggests that fluctuations in animal populations in nature are the rule rather than the exception. To understand the reasons for these fluctuations it is necessary to understand how the size of population of animals in nature is determined.

The size of a population of any species is the result of the interaction of two sets of forces often designated as biotic potential and environmental resistance. Biotic potential may be defined as the potential power of reproduction of a species under ideal conditions. This power is always tending to increase the size of a species' population. The increase is resisted by such factors of the environment as food scarcity, predators, disease, and unfavourable meteorological conditions. Such environmental factors together constitute the environmental resistance. Since it is difficult to conceive of the biotic potential, that is the inherent reproductive capacity of a species, as varying except as a result of environmental changes, it may be assumed that all population fluctuations are due to environmental changes.

A striking illustration of the way in which populations react to environmental changes was afforded by Manitoba's muskrat management project. Following the construction of a system of dams, dykes, and canals, as a result of which suitable muskrat habitat was restored in dried up marshes, the muskrat population in one area increased from 1,000 to 200,000 in four years.

The extent to which animal populations can increase when food is unlimited is exemplified by an Australian experience during the First

World War, when 544 tons of mice, thought to represent thirty-two million animals, were caught around stacks of bagged wheat awaiting shipment to Great Britain (Elton, 1942).

Many illustrations of the population potentialities of animals have been cited. Bailey's (1924) figure for *Microtus,* the meadow mouse or vole—one million at the end of one year from a single pair at the beginning, if given ideal conditions—is a striking example of the reproductive powers of a common Canadian mammal. With such figures in mind we are perhaps prepared to be surprised, not that populations fluctuate but that fluctuations are not more violent.

Under natural conditions, on the average, only two offspring from a pair of animals during their lifetime reach maturity. If more than two on the average survived to take the place of the two that produced them, the population of that species would in time fill the earth. On the other hand, if fewer than two survived, on the average, the species would gradually die out. The environment is continually changing, leading to the production and survival of a varying number of young and adults from time to time. This results in variations in the size of populations which, over a period of years, fluctuate about a mean.

When the population of a species attains unusual abundance, it always results from some lessening of the environmental resistance usually through provision of abundant food, or reduction in numbers or absence of predators, or both.

The history of moose on Isle Royale, Lake Superior, affords one example of the type of experience which has been repeated by many kinds of animals under many different conditions. Although there may have been moose on the island in earlier times, their recent history there appears to have begun during the winter of 1912-13 when a few animals made their way to the island over the ice which formed that year between it and the Canadian mainland, thirteen miles away at the nearest point. With plenty of food available and in the absence of hunters, wolves, or other large predators, moose increased so that when Murie (1934) made his survey in 1930 he estimated a population of between one and three thousand. The size of the island is 220 square miles and at that time the vegetation gave many evidences of being over-browsed. Between 1929 and 1935 the moose population on Isle Royale decreased from a high of one to three thousand to about two hundred (Shaler and Krefting, 1946) presumably as a result of the depleted food supply which, in turn, had resulted from the over-population.

An example from the opposite end of the size-scale of mammals was afforded by a California experience with mice. In 1926 a plague of mice involving at least tens of millions and possibly hundreds of millions spread over the country-side from their point of origin in the dry bed of Buena Vista Lake. Here during the previous year or two the multiplication of the mice had been favoured by abundance of food and scarcity of predators. The plentiful food supply was in the form of barley and Kaffir corn left on the ground after harvest. The scarcity of predators was in part due to an intensive poison campaign against coyotes which had been carried on during the previous year or two. Other predators including kit foxes and skunks had been poisoned as well as coyotes. Protection from winged predators was afforded the mice by Kaffir corn stalks from which only the heads had been cut. Finally the mice (nearly all *Mus musculus* but some *Microtus californicus*) left their breeding grounds and spread out over the surrounding farms. The descriptions of the numbers of mice involved are almost unbelievable. In one trench made in the path of the migrating mice an average of between fifteen and sixteen dead mice per linear foot was found on the third day after the trench had been made. This trench was about five miles long, and it was computed that one-half million mice had been killed by eating poisoned grain placed in it. "At night, on the highway . . . the illumination from the headlights of one's car revealed hundreds of live mice at any given instant. . . . Truly, the number of mice was almost unbelievable, and one who has not seen this or a similar outbreak can scarcely comprehend the vast numbers that can occur in a given area of limited extent. Certainly the numbers were to be reckoned in tens, and possibly in hundreds, of millions."

Sometimes the introduction of an animal into a favourable new environment is followed by spectacular increases in numbers. The increase and spread of rabbits in Australia is a well-known example but we have several closer to home.

The European starling introduced into Central Park, New York City, in 1890 and 1891, arrived in Ontario in 1919 and in about fifteen years, according to L. L. Snyder, became the most abundant bird in Ontario south of Lake Simcoe.

The history of the smelt *(Osmerus mordax)* in the Great Lakes affords another striking example of the attainment of a large population by an introduced species (Dymond, 1944). It was first recorded from Lake Huron in 1925 and first spawning runs in streams of the north shore occurred in 1932. By 1941 there was not a stream, large or small, along all of Georgian Bay that was not visited at spawning time. In some the smelts were so abundant that sufficient were caught to fill steel-bodied gravel dump trucks in half an hour. From two to four tons were taken from one creek in three hours' time on more than one occasion. In this case, as in that of many others when animals become very abundant, a drastic decline in population was experienced. In the latter part of October, 1942, tremendous numbers of dead smelts, described as "a solid white sea of dead smelts," were seen floating on the water in the North Channel. On many parts of the north shore of Manitoulin Island, dead smelts were piled to a depth of at least one and a half feet. As a result, the next spring spawning runs were greatly reduced and in many streams where large runs had occurred in previous years smelts were entirely absent. (Stevenson, 1944.)

Two types of population fluctuation may be recognized—the periodic and the non-periodic. Examples of the latter are afforded by such occurrences as the California mouse plague, and the appearance of moose in Isle Royale and smelts in Lake Huron. In such cases some unusual combination of favourable conditions brings about an exceptional abundance of some species which, when the favourable conditions cease to exist either through the action of the animals themselves or otherwise, declines, often drastically.

PERIODIC FLUCTUATIONS

The populations of many animals undergo periodic fluctuations, that is changes from abundance to scarcity which recur at rather regular intervals. It is to Elton (1924, 1927) that we owe the great development of interest in this phenomenon although Poland (1892), Macfarlane (1905), Seton (1911), and Hewitt (1921) had previously drawn attention to it.

Reference has already been made to the varying hare or snowshoe rabbit *(Lepus americanus)* whose populations have reached peaks of abundance usually at intervals of nine or ten years for at least as long as Hudson's Bay Company records are available (Fig. 2). During the period 1856 to 1934 there were nine occasions on which the numbers of hares reached peak proportions (MacLulich, 1937). On each occasion these peaks were followed by drastic reductions. This represents an average of 9.7 years between maxima. In three cases the period between maxima was 10 years, in two cases it was 9 years, in two others 11 years, and in one 8 years. The ruffed grouse *(Bonasa umbellus)* has a periodic fluctuation in population corresponding closely to that of the varying hare, namely between nine and ten years on the average (Clarke, 1936).

Another remarkable periodic phenomenon connected with animal populations is the arrival of snowy owls in southern Canada and northern United States every four or five years. There is strong circumstantial evidence for the conclusion that the emigration of these owls from their Arctic homeland is associated with the attainment of a population peak following an increase in the numbers of their staple food animals, the lemmings. This conclusion is based on the occurrence of maximum populations of Arctic foxes in the north in the years when snowy owls appear in southern Canada. Lemmings are the staple food of both Arctic foxes and snowy owls. Gross (1931) compares the two occurrences as shown in Table I.

TABLE I

YEARS OF MAXIMUM NUMBERS OF ARCTIC FOXES AND OF SNOWY OWL EMIGRATIONS

The years of maximum numbers of Arctic foxes at Fort Chimo	*Winters of noteworthy appearances of snowy owls in southern Canada and northern United States*
1872	
1876	1876-7
1879	
1882	1882-3
1887	
1890	1889-90
1893	1892-3
1897	1896-7
1901	1901-2
1905	1905-6
1909	
1913	
1917	1917-18
1921	
1926	1926-7
1930	1930-1

Large flights of snowy owls have also appeared in 1934-5, 1937-8, 1941-2, 1945-6. Mr. L. L. Snyder of the Royal Ontario Museum of Zoology reports that estimates of the comparative numbers involved in recent flights are as follows, the number of the 1926-7 flight being represented arbitrarily by the figure 10:

1926-7	10
1930-1	6
1934-5	4
1937-8	2
1941-2	5
1945-6	20+

Following is a list of Canadian animals whose population fluctuations have been shown to be definitely periodic in frequency.

TABLE II

SPECIES OF CANADIAN ANIMALS SHOWING PERIODIC FLUCTUATIONS IN ABUNDANCE

Species	*Usual period*	*Extreme range*	*Authorities*
MAMMALS			
Lepus americanus	9-10	8-11	Poland (1892), Macfarlane (1905) Seton (1911), Hewitt (1921) Elton (1924), MacLulich (1936)
Ondatra zibethica	9-10	?8-12?	Elton and Nicholson (1942a)
Microtus pennsylvanicus	4	?	Hamilton (1937), Banfield (1946)
Lemmus trimucronatus *Dicrostonyx hudsonius*	4		Elton (1924, 1942)
Vulpes fulva	9-10	8-13	Hewitt (1921), Cross (1940)
Alopex lagopus	4	3-6	Hewitt (1921, Elton (1924, 1942)
Martes americanus	9-10	8-11	Hewitt (1921)
Martes pennanti	9-10	8-11	Hewitt (1921)
Mustela vison	9-10	6-12	Hewitt (1921)
Lynx canadensis	9-10	7-12	Hewitt (1921), Elton (1924, 1933b) Elton and Nicholson (1942b)
BIRDS			
Accipiter gentilis	9-10		Speirs (1929)
Buteo lagopus	4	3 5	Speirs (1929)
Bonasa umbellus	9-10		Criddle (1930), Clarke (1936)
Lagopus lagopus	9-10	9-12	Clarke (1936)
Tympanuchus cupido	cyclic		Leopold (1931)
Pedioecetes phasianellus	9-10		Criddle (1930), Snyder (1935)
Bubo virginianus	9-11		Speirs (1939)
Nyctea scandiaca	4	(2?) 3-5 (6?)	Gross (1931, 1937) Speirs (1939), Snyder (1943)
Lanius excubitor	4	(3?) 4-5 (6?)	Davis (1937), Speirs (1939)
Pinicola enucleator	5-6		Speirs (1939)
FISH			
Salmo salar	9-10		Huntsman (1931), Griswold (1929) Phelps and Belding (1931)
Oncorhynchus nerka	4 in Fraser River watershed		Mooney (1861), Babcock (1902) Foerster (1929)
Oncorhynchus gorbuscha	2		Pritchard (1937)

Although the periodicity of *Microtus* has not been established in Canada, Banfield (1947) has recorded evidence that strongly suggests a cycle. An unusually high peak of abundance of these mice occurred in southern Ontario in 1936 and farther north in 1937 (Whelan, 1939). Banfield's observations at Toronto suggested peaks in 1935, 1940, and 1945. A historic "plague" of voles occurred in Nova Scotia in 1815 (Patterson, 1887) during which the mice were so numerous that "over acres and acres they left not a stalk standing nor a grain of wheat to reward the labour of the farmers. . . . Farmers had to sell off a great part of their stock at low prices."

CAUSES OF NON-PERIODIC FLUCTUATIONS

Non-periodic fluctuations in populations are probably to be accounted for through the action of some unusually favourable or unfavourable environmental condition or combination of conditions. The combination of conditions favouring the increase of mice which led to the California mouse plague has already been discussed.

The occurrence of abundance of a particular type of plankton at the time and place when and where newly hatched fish occur has been suggested as the explanation for the origin of unusually successful year-classes which have been shown to characterize many species of food fishes in European waters (Hjort, 1926).

The clue to the explanation of the wide but irregular fluctuations in the populations of many marine fishes was found by Hjort (1914) in the occurrence of striking differences in the strength of different year-classes of herring in Norwegian waters. He found for instance that the herrings spawned in 1904 were so abundant that they dominated the Norwegian herring fishery for a long period of years. Other good years were 1913 and 1918 while intervening years were poor. The same phenomenon of unusually successful and also unusually unsuccessful year-classes has been found to occur with many of the important food fishes in European waters. Sometimes the members of one year-class will be fifty or sixty times as numerous as those of another. That similar conditions occur in Canadian waters has been shown by the work of Hart (1933, 1943), Tester (MSS.), and others in connection with researches of the Fisheries Research Board of Canada, as will be outlined later.

Many of the wide fluctuations between abundance and relative scarcity which occur in Great Lakes fisheries are probably to be explained on the basis of great differences in the strength of year-classes. For instance the present abundance of lake herrings in Lake Erie is known to consist largely of a single year-class. When the members of this year-class have been caught or have died off, lake herring fishing will again be poor unless another successful brood year appears.

Some light was thrown on the question as to the stage at which losses occur in an anadromous fish, the pink salmon *(Oncorhynchus gorbuscha)*, by the results of studies carried out on McClinton Creek, Queen Charlotte Islands, by Pritchard (1938) under the auspices of the Fisheries Research Board. In connection with these studies, a fence and traps were constructed by means of which all adults entering and all young leaving the experimental stream were trapped, for counting. Table III gives the number of adults and young respectively entering and leaving during each year of the experiment. There is in this case a single population concerned, the seaward migrants of one year producing the adults of the following year. We therefore have information on the size of the population of a year-class at three stages, as we know (1) the number of parents, (2) the number of resulting seaward migrants, and (3) the number of resulting adults. Table III gives this information for each of the years during which the experiment was carried on. It indicates that during the period covered there was a fifteen fold variation in the size of the run.

TABLE III

Number of Pink Salmon at Three Stages in the Life History of a Year-Class
(Fry from 1930 spawning produce 1932 adults, etc.)

	Adults	*Seaward migrating fry*	*Per cent of eggs producing seaward migrating fry*	*Percent of fry producing adults*
1930	66,153	5,384,000	10.6	0.29
1932	15,600	2,300,000	17.3	6.74
1934	155,196	12,600,000	9.0	0.42
1936	52,312	3,675,000	6.9	0.29
1938	10,577	2,020,000	23.8	1.75
1940	35,525	5,060,000	19.0	0.73
1942	36,893			

While there was a wide difference in the percentage of eggs which produced seaward migrants, this factor is apparently not the most important one so far as the number of adults returning to the stream is concerned. This is illustrated by the fact that roughly 2¼ million seaward migrants in 1932 (the second smallest number of fry found during the seven cycles) produced the largest population of adults, namely 155,196, whereas more than 12½ million seaward migrants in 1934 produced only 52,312 adults in 1936. It is of course not certain that all of the adult progeny from a given stream return to it when they mature or that all adults entering a stream were produced in it. It is obvious however that the size of the run of adults to the experimental stream bore little relationship to the number of young of the year-class to which they belonged. This lack of correlation was due more to the extent of the loss from seaward migrant to returning adult than to the loss from egg to seaward migrant.

In an effort to secure information on the extent to which fish return to their natal stream, a large number of fry were distinctively marked in several years by removal of certain fins and rewards were offered for the detection of fish so marked in other parts of British Columbia and in Alaska. In all cases most of the marked adults that were identified were found in McClinton Creek. Some were taken by commercial fishermen in areas from which it is reasonable to expect they might have returned to the home stream. A few were captured in areas from which return was quite improbable. That is, of 108,000 progeny of the 1932 spawning which were marked, 3,285 were subsequently recovered, 2,950 of them in the parent stream; of the others, only 7 were taken outside the Queen Charlotte Islands area.

Mortality from seaward migrant to the entrance of the adult into the natal stream will include both natural and fishing mortality. In the McClinton experiments it was impossible to estimate variation in fishing mortality from year to year. The results of the experiment are therefore not conclusive but they strongly suggest great differences in natural mortality in the sea stage of the life history of the pink salmon.

Causes of Periodicities in Population Fluctuations

Several explanations of the regularity which characterizes many fluctuations in animal populations have been suggested. Lotka (1920) and Volterra (1926) on the basis of mathematical theories have shown how oscillations are inherent in some population systems and Gause (1934) has shown that under ideal experimental conditions some of their mathematical equations seem to be realized. However the value of these mathematical theories in the study of populations in nature is still in doubt.

The belief that there was some sort of relationship between the sun-spot periodicities and the periodicities of hares and grouse was rather widely held for a time (Elton, 1924; De Lury, 1930; Wing, 1935). MacLulich (1937) is generally believed to have disposed of this theory so far as the hare is concerned when he showed that the animal and solar cycles are of different lengths and that therefore, although there are recurring periods during which the animal peaks correspond more or less closely to the sun-spot maxima, these are followed by periods when animal maxima are in phase with sun-spot minima. Although MacLulich's arguments have convinced many (Elton and Nicholson, 1942a) the sun-spot theory appears still to fascinate others (Clements and Shelford, 1939). It is the belief of the present author that the explanation of the regular periodic fluctuations in some animal populations can be found without calling in the aid of extra-mundane factors.

Leaving aside the Atlantic and Pacific salmons, which require a separate discussion, the animals whose populations have been shown to present regular periodic fluctuations belong to two categories: (1) predators whose periodic fluctuations obviously depend on the periodic fluctuations of their prey and (2) rodents or other essentially plant-eating animals whose periodicities have not been shown to depend on any periodic factor in their environment.

The dependence of the periodicities of a number of predatory mammals and birds on the periodic fluctuations in the populations of their prey is obvious. The dependence of the Canada lynx *(Lynx canadensis)* nine- to ten-year periodicity on the corresponding periodicity in the hare (*Lepus americanus*) is generally admitted. To a surprising extent the food of the lynx is largely restricted to hares. The correspondence between the curves representing the number of lynx and the number of hare skins from Canada sold in London by the Hudson's Bay Company is remarkably close. As is to be expected in the case of a predator the curves representing its population increase are often one year to the right, i.e. later, than the corresponding hare curves.

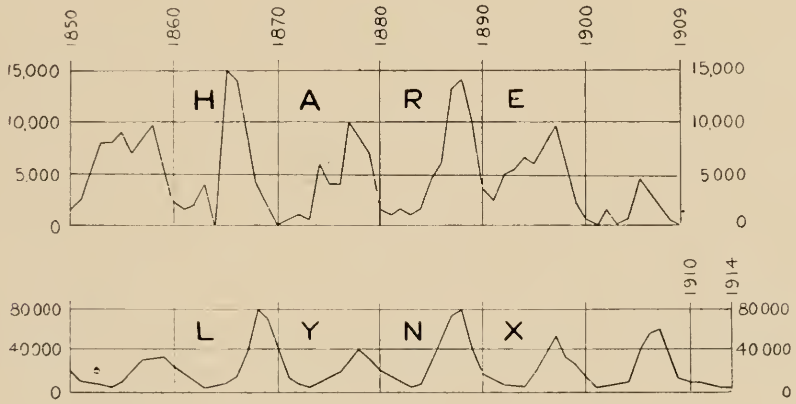

Figure 2.—Correlation between periodic fluctuations of hare and lynx populations as represented by Hudson's Bay Company fur returns, 1850-1909. (Based on Hewitt, 1921.)

The fact that coloured foxes (*Vulpes fulva*) and the marten have a four-year cycle in the Arctic and a nine- to ten-year one farther south is strong evidence for the belief that the length of the cycle in predatory forms depends on the periodicity of the prey species. The food of fox *(Vulpes fulva)*, marten *(Martes americana)*, fisher *(Martes pennanti)*, and mink (*Mustela vison*) is not so restricted to hare as it is in the case of the lynx. It should be remembered, however, that the fur statistics used to establish the periodicities of these animals are for northern Canada where the variety of prey is much more restricted than it is farther south. One indication that marten numbers are influenced by hares is afforded by the fur statistics of Douglas for British Columbia as reported by Cowan (1938). On the mainland marten peaks occurred in 1826, 1836, 1845, and 1853, whereas on Vancouver Island, where there are no hares, marten peaks occurred in 1842, 1852, 1855, and 1857. It is generally accepted, I believe, that all of these predatory mammals prey more or less extensively on hares when the latter are available. The same is true of two large predatory birds, the goshawk (*Accipiter gentilis)* and horned owl *(Bubo virginianus),* whose periodicities correspond with that of the hare. No one, I believe, questions the direct connection between the four-year periodicity of the Arctic fox (*Alopex lagopus*) and snowy owl (*Nyctea scandiaca*) and the corresponding periodicity of the lemming *(Lemmus trimucronatus* and *Dicrostonyx hudsonius*). The periodicity of the rough-legged hawk probably also depends on the lemming periodicity.

In the case of carnivorous mammals and birds, it is the size of the population of their prey animals that determines the size of their populations and not *vice versa.* Errington (1946) in his exhaustive review of predation and vertebrate populations concludes that "regardless of the countless individuals or the large percentage of the population that may annually be killed by predators, predation looks ineffective as a limiting factor to the extent that intraspecific, self-limiting mechanisms basically determine the population levels maintained by the prey." The fact that "among the mammals and birds, the numbers of those tolerant of crowding appear most influenced by predation" is possibly significant in connection with the problem of periodicities as we shall see later.

We therefore narrow down our problem of accounting for the regularity in the population fluctuations among Canadian birds and mammals to that of accounting for the periodicities of relatively few, including the varying hare, muskrat, meadow mouse or vole, lemmings, ruffed grouse, etc.

The following characteristics of these animals and of their periodicities appear to be significant.

1. The variation in the length of cycle from time to time within the same species and the rather wide difference in time at which peak populations are reached in different parts of the country.

2. The lack of uniformity in the average length of the cycle in different species—four years in lemmings and *Microtus,* six in pine grosbeak and nine or ten in the hare, the muskrat, and the grouse and its relatives.

3. The fact that these are all Arctic or boreal animals.

4. The fact that the mammals are all rodents and the birds with the exception of the pine grosbeak all grouse or relatives of the grouse.

Although the periodicity of the hare must be recognized as remarkably regular, it is easy to over-emphasize the regularity. As MacLulich

(1937) has pointed out, the Hudson's Bay Company records on which these figures are based are for a limited area of Canada, namely the region surrounding Hudson Bay. When the whole of Canada is considered, the peaks do not coincide but occur in different years in different areas. MacLulich found that the onset of diminution of numbers, which is more definitely determinable than the attainment of maximum numbers, occurred in south-eastern Ontario in 1932, in central Ontario in 1933, from Temiskaming to Kenora in 1934, in the northern part of the clay belt in 1935, on the coast of James Bay in 1934 and in the southern part of the Patricia District in 1933.

Clarke's (1936) work on the ruffed grouse also showed that the periodicity of this species when studied carefully is not nearly so regular as might be supposed. Clarke found the first evidence of diminution of numbers in Canada in the nineteen-thirties occurred in 1930 in Nova Scotia. In 1932 all the reports of decrease came either from the east coast or the north-west while the first evidence of cyclical decrease in Ontario came in 1933. The south-western part of the province, which was the first to suffer a decrease in hares, was the last to record a decrease in grouse. When the conditions of grouse abundance in areas of Canada outside Ontario were considered, differences in the year of commencement of the diminution in numbers were found to extend over a number of years equal to at least half of the periodicity of the cycle. Clarke considered it possible that grouse might be found in any given stage of the cycle in some part or other of North America in any given year.

Although the periodicity of the fox is secondary, depending on that of the hare, perhaps influenced by fluctuating abundance of mice, a study of its periodicity by Cross (1940) contributes to an understanding of the extent of variation in the length of the period of population fluctuations and of the variation in the time at which peaks are attained in different areas. This study shows that in the case of the red fox, periodic fluctuations in numbers are not province-wide but are definitely regional phenomena. Cross's records covered a period of twenty years, 1916-35, and included records from thirty-four trading posts of the Hudson's Bay Company in northern Ontario and of more than 100,000 fox pelts. He demonstrated that a large proportion of the posts reached a maximum catch of foxes in years other than the peak years. For instance the maximum for the whole province was reached in 1917, in 1926, and in 1936 yet in 1917 only 52 per cent of the individual posts reached their maximum; in 1926 the corresponding number was 50 per cent while in 1936 it was only 30 per cent. There was also a wide variation in the interval between peaks at different posts. Between the first and second of the three peaks discussed the interval was:

8 years in 14 per cent of the posts
9 years in 24 per cent
10 years in 43 per cent
11 years in 14 per cent
13 years in 5 per cent

Table II indicates the extent of variation (extreme range) in the length of cycles in different species.

It has long been recognized that periodic fluctuations in animal populations are virtually confined to the northern part of the northern hemisphere and are especially characteristic of the Arctic, not only in America but also in Europe and Asia where the same species—lemmings, snowy owls, and Arctic foxes in America and lemmings and snowy owls in the Old World—undergo violent periodic fluctuations. The phenomenon is still pronounced in the north temperate region but disappears southward. Cowan (1938) on the basis of records in the note-book of James Douglas reports that in the southern part of British Columbia rabbits (hares?) never underwent the extreme fluctuations in numbers characteristic of the north. This is reflected in the fact that lynx numbers increased a hundred fold from lowest ebb to highest peak in the northern part of the province, through an intermediate increase of fifty fold in the intermediate latitude of Langley to a relatively stable population (an increase of but twenty fold) at Fort Vancouver three hundred miles farther south.

Finally, the fact that the "key industry" animals whose fluctuations in numbers are periodic are all rodents or grouse-like birds (with the exception of the pine grosbeak) is undoubtedly significant.

Briefly the theory here offered to account for the periodicity in the fluctuations of the populations of lemmings, hares, voles, grouse, etc., is that the biotic potential of these animals is definitely greater than the normal resistance of the environment in which they live. In other words they are endowed with too high a reproductive capacity and it is the monotony or relative uniformity of the Arctic and far northern environment that accounts for the regularity with which they increase to the unstable level of numbers which brings about the periodic decline.

It should be emphasized that it is the regularity of the events producing a decline in populations that must be accounted for. Any small population of an animal placed in a suitable environment will normally increase in size. Either one of two occurrences normally brings the increase of population of the animals under discussion to an end and produces a decline. One of these is emigration, the other is disease.

Emigration as a Factor in Population Fluctuations

Emigration as a means of population reduction occurred in the case of the California mouse plague already referred to, but perhaps the most famous example is afforded by the lemmings of Scandinavia. Elton's (1942) description gives a picture of these emigrations. "In the big years lemmings begin to travel down the mountain sides and valleys through the tree belt . . . out over the lowlands, crossing fields and lakes and rivers and passing through busy towns, until those that survive reach the coast. Here they swim out . . . many drown . . . and are cast ashore in drifts. . . . After a year or two, and mostly much sooner, all of them are dead. There remain a number of their depleted populations on the high hills, as nuclei of further waves of lemmings."

There are comparatively few records of lemming emigrations in Arctic America. Anderson (1937) suggests that the lack of such records is due partly to the fact that there are fewer observers in Arctic Canada and partly to the comparative flatness of the Canadian Arctic generally, which does not give opportunities for concentration of the animals in settled regions at the base of mountains as in Norway, Sweden, Finland, and Russia. The following three records, however, attest the fact that migrations do occur in our Arctic. Rae (1890) reports that when travelling in June, 1851, southward from the Arctic coast along the west bank of the Coppermine River and north of the Arctic circle he met with thousands of lemmings speeding northward. A big migration of *Lemmus* at Point Barrow, Alaska, in 1888 is recorded by Allen (1903) and Anderson (1935) says that Captain Berthé witnessed a big migration of *Lemmus trimucronatus* in May, 1926, at Baker Lake.

Snyder (1935) has recorded a spectacular emigration of sharp-tailed grouse *(Pedioecetes phasianellus)*. In the autumn of 1932, grouse of this species arrived in numbers in many sections of northern Ontario where they are normally absent or not very common. They were observed near the end of October passing over Moosonee in vast flocks that reminded the observer "of the stories he had heard of the passenger pigeon in years gone by." This unusual migration continued at approximately the same rate for about three weeks. While the evidence is not as conclusive as could be desired, largely owing to the lack of observers in the area from which the grouse originated, there is reason to believe that this emigration followed a peak of numbers in the area concerned. A similar emigration had occurred in 1896.

Emigration, as already noted, occurs every four years on the average in the case of the snowy owl, presumably at times of peak abundance. Although less spectacular, periodic emigrations of goshawks and great horned owls also occur.

Other animals which show periodic fluctuations in population but do not normally emigrate, occasionally do emigrate. That mass movements of varying hares sometimes occur is attested by Cox (1936) who witnessed such a movement at the time of hare abundance in northern Minnesota. As is usual in such cases, the animals all moved in one direction. The numbers involved are suggested by the fact that at the farther edge of a large lake which the hares crossed in their travels "thousands" had fallen victims of hawks and owls that had evidently gathered there to prey on them.

Elton (1942) reports that the Arctic fox occasionally moves southward in numbers. In 1922 they reached as far as the Canadian Labrador. In the spring of 1923 one was shot on the coast of Cape Breton Island. Emigrations occasionally occur also among lynx, marten, and coloured foxes.

The phenomenon is also known among animals whose populations are not cyclic; for example, Seton (1928) records the movements of "immense numbers" of gray squirrels *(Sciurus carolinensis).*

Disease as a Factor in Population Fluctuations

That disease is commonly responsible for the decline in the numbers of animals which have reached a high level of population has long been recognized. Darwin (1859) observed that "when a species, owing to highly favourable circumstances, increases inordinately in numbers in a small tract, epidemics—at least, this seems generally to occur with our game animals—often ensue."

Even in the case of animals where shortage of food resulting from over-population leads to population reduction, this is often brought about through the action of parasites and disease rather than through actual starvation. Malnutrition as well as crowding favours the spread of parasites and disease organisms.

That disease is the factor responsible for the rapid decline in the numbers of hares following the attainment of their population maxima is well established. From MacLulich's (1937) excellent summary of the evidence we learn that a variety of diseases are responsible and that the particular disease or combination of diseases varies from cycle to cycle and from place to place during the same cycle. He found that a blood-sucking stomach worm (*Obeliscoides cuniculi*) caused an epidemic at Smoky Falls, Ontario, in 1935.

Green (1935) once suggested that tularaemia might be responsible for the periodic decline in hare population (see also Huntington, 1932) and later (1939) suggested a "shock" disease as the explanation. MacLulich showed that while tularaemia occurred among varying hares in widely separated parts of Ontario it was not present even at the time of their dying-off in any large percentage of the population.

Clarke (1936) found disease to be the immediate cause of the periodic decrease in ruffed grouse populations. Although several parasites and diseases were found, the only organism significantly associated with the diminution of grouse numbers during the cycle which he investigated was a blood protozoon, *Leucocytozoon bonasae*.

Elton (1935b) has described the periodic epidemic among *Microtus agrestis* in England. A protozoan infection of the brain due to *Toxoplasma* has been shown to be the cause. An epidemic among American voles has been recorded by Hamilton (1937). At the time of the 1926-7 California mouse plague already mentioned, Wayson (1927) isolated the causative bacillus of mouse septicemia or swine erysipelas (sometimes considered identical) from morbid microtines involved in the outbreak. Evidences of disease among voles are recorded in connection with the famous Nova Scotia plague of mice in 1815. It is recorded (Patterson, 1887) that in the autumn the mice "became languid, scarcely able to crawl. One could trample them under his feet and finally they died in hundreds, so that they could be gathered in heaps."

The relation of population density to the spread of disease was pointed out by Ross (1911) in connection with the control of malaria. He formulated mathematically an equation of the struggle for existence between malaria plasmodium and man with participation of the mosquito. Disease is always present but reaches plague proportions only after the host has passed a certain threshold of numbers. Fluctuations in weather and other ecological conditions may modify the length of time needed to reach the required level of numbers. The fundamental periodicity, however, is probably determined by the time required to reach the threshold of numbers necessary for disease spread.

EMIGRATION PHENOMENA

There is strong evidence that emigration, like disease, is the result of a certain rather high density of population. The most obvious suggestion as to the initiating factor in emigration is that it follows exhaustion of the food supply. However, observations have usually failed to find evidence of lack of food in the case of emigrants. Snyder (1935) reports that the specimens of sharp-tailed grouse collected during their 1932 flight were in good physical condition. Speirs (1939) quotes C. E. Hope of the Royal Ontario Museum of Zoology, who has examined a large number of goshawks and horned owls collected during their periodic immigration into southern Ontario, as stating that there is no evidence from the birds' condition to indicate that lack of food caused them to come south. Similarly the snowy owls which periodically reach southern Ontario have never been found to show signs of malnutrition.

Uvarov (1921, 1928) has thrown considerable light on the factors involved in the spectacular emigrations which have characterized the populations of locusts in many parts of the world. His studies show conclusively that food shortage plays no part in initiating locust emigrations. The insects leave their breeding grounds while food is still plentiful and pass through and over areas of abundant food on their flights. On the other hand, the phase during which the locusts undertake mass movements is produced as a result of the crowding of a large number of individuals in a limited space.

The insects concerned exist in two quite distinct phases, a solitary phase and a gregarious phase, which differ not only in behaviour but also in morphological and colour characteristics to such an extent that they have been regarded as different species. The two phases are connected by a transitional phase of intermediate characteristics. Uvarov believes that either of the extreme phases can be transformed into the other but Allee (1931) does not think it has been clearly proved that the transformations from one phase to another do actually take place on a large scale and to a convincing degree. While the solitary phase consists of isolated individuals, the gregarious or swarming phase forms dense emigrating swarms. It is stated that, once the development of the swarming phase has begun as a result of crowding, this process can only increase in intensity because the bands once formed unavoidably grow during their wanderings owing to fusion with other bands. Only sufficiently large swarms emigrate.

Uvarov's description of emigrating locusts reminds us of the accounts of emigrating lemmings and other animals. "The relentless march of such masses of hoppers, regardless of obstacles, creates an impression of some dark purpose, of a movement towards an objective, and has led to numerous more or less fantastic explanations of the cause of movement based on the imagination of the observer and not on the facts. Obstacles to the moving bands, in fact, do not seem to exist; they pass over hillocks and boulders; holes and ditches in the ground are filled with the bodies of the first coming hoppers, and their comrades pass over them as if over level ground. . . . Across canals and streams the bands swim to the other side and continue their march."

The emigratory behaviour of locusts therefore has many features in common with that of lemmings and in many respects in both animals is in striking contrast to the behaviour shown in their breeding territories. Similar difference in behaviour is recorded by Kennicott as quoted by Seton (1928) in the case of the gray squirrel *(Sciurus carolinensis)* which formerly undertook mass movements. Kennicott says: "Immense numbers congregate in autumn and move off together, continuing their progress in the same general direction, whatever it may be . . . not even turning aside for large streams. Ordinarily averse to entering the water, they now take to it boldly, and though swimming with difficulty, manage to cross broad rivers like the Niagara and the Ohio, though many are drowned in the attempt." During one of these migrations "innumerable squirrels" are said to have swum across the river near Niagara and landed near Buffalo.

Seton was unable to find any records of these mass movements of squirrels after 1870 but Hamilton (1939) records them in Connecticut and New York in 1933 and 1935. The fact that such movements are rare now as compared with former times suggests that they were a feature of the squirrels' behaviour before their populations were reduced through the destruction of the hardwood forests which provided them with such abundant food in earlier times.

Whether the "crazy" flight of the ruffed grouse is another manifestation of abnormal behaviour associated with emigration resulting from crowding is not clear. Two characteristics suggest that it is. Although grouse do not normally form large flocks, Clarke (1936) quotes an observer as saying that he had seen the grouse cross the Ottawa River "in large numbers." The other circumstance which suggests a similarity of these "crazy" flights to certain characteristics of the mass emigration often observed among other species is their abnormal nature, indicated by their popular description as "crazy."

The evidence therefore suggests that emigration may not be due to food shortage but is rather a reflection of abnormal behaviour patterns resulting from crowding.

Allee (1931) in his book on *Animal Aggregations* shows that, while under many conditions there are distinctly beneficial results from crowding, when it is too great it is harmful, especially for poorly integrated groups of animals.

The intolerance to crowding shown by certain species may be related to the phenomenon of territoriality (Nice, 1933). If this is the case, it might explain the fact that some animals when crowded emigrate before food is exhausted while others, as for example deer, remain in crowded areas until the food supply is so reduced that they succumb to starvation or diseases favoured by malnutrition. In the case of dense populations there appears to be a race between disease, emigration, and starvation as to which is to reduce the numbers, with the decision determined largely by the reaction of the species to crowding.

The reaction of animals under crowded conditions is sometimes referred to as arising from intraspecific tension or population pressure. The latter expression may have been suggested by a comparison of the outward movement of the animals from their home ranges to an explosion. The fact that the latest emigration of snowy owls, which was the largest on record, carried the birds the farthest indicates that the comparison of emigration to an explosion is, in that respect at least, appropriate.

That the whole phenomenon is far from simple is indicated by the fact that in spite of the emigratory animals acting as if they were trying to get away from crowded conditions, they sometimes move in vast flocks. The factors involved in the initiation and continuance of emigratory movements are complex and will provide fascinating problems for students of animal behaviour.

Periodicity in Attainment of High Population Levels

Whether the factor which at the end of a fairly definite number of years brings about the population decline is disease or emigration, it appears to be initiated by conditions arising from the attainment of a rather high level of population density. Why is it that in the case of the animals under discussion—lemmings, voles, hares, grouse, etc.—this critical level of numbers is always reached after roughly the same number of years? A species placed in a perfect environment without variation in any of its components would always reach the same level of numbers in the same period of time, while variation in the action of any environmental factor would produce a variation in the length of time required to reach a given level of numbers unless compensated for by variation in some other factor. These species will show the more regularity in the period required to reach a certain level of numbers the less they are affected by environmental changes.

While the Arctic environment cannot be described as uniform, it is in a number of respects much more nearly uniform than environmental conditions farther south. This is true for instance in the matter of predators. The Arctic lemming has comparatively few predators, these including the snowy owl, rough-legged hawk, gyrfalcon, and Arctic fox, whereas a rodent of comparable size in the austral region of North America has a host of predators, such as red and gray foxes, coyote, raccoon, opossum, spotted and striped skunks, weasel, mink, badger, shrews, marsh, red-shouldered, and red-tailed hawks, barn and barred owls, as well as several species of snakes including a number of species each of king snakes, milk snakes, gopher snakes, rat snakes, and rattlesnakes. Moreover there are in the environment of the austral rodents many buffer animals which share with them the predator pressure of the carnivores including meadow mice, white-footed mice, pine mice, pocket mice, harvest mice, jumping mice as well as many somewhat larger forms such as chipmunks, cotton rats, kangaroo rats, pocket rats, and wood rats. The effect of "buffers" on the populations of other animals has been pointed out by Errington (1945). So far as the predator part of the lemming's environment is concerned, it must exert a fairly uniform pressure, the Arctic foxes and snowy owls increasing in fairly direct ratio to the lemmings since their populations are dependent on that of the lemmings. In the case of austral rodents, the populations of their predators are not so directly dependent on that of a single species but on the populations of a variety of prey. Similarly the predator pressure is not exerted on a single species but is buffered by a variety of other prey animals. There is therefore not the same uniformity of relationship between predator and prey in the south as in the north.

It is unlikely that the character of the environment is alone responsible for the regularity with which the populations of these animals reach the critical density which initiates the decline. The reproductive capacity and habits of the animals probably also contribute to the cumulative increase which characterizes their normal population dynamics. It is undoubtedly significant that the only Canadian mice which have been shown to exhibit periodic fluctuations in population are so closely related genetically. Their habit of burrowing beneath the snow tends no doubt to insulate them from the effects of some of the variations in climatic conditions.

The suggestion that the character of the animal as well as the character of the environment has a bearing on the cyclical nature of their population histories is supported by the fact that the smaller animals with the higher biotic potential have the shorter cycles. Lemmings and *Microtus* attain the critical population level in four years on the average as compared with nine or ten in the case of hares, muskrats, and grouse.

In contrast to the theory which explains the regular periodicity in population changes as the result of something regularly periodic in the environment the theory here offered would explain the variations in the length of the cycles—two to five years in lemmings and eight to thirteen in hares—as due to variations in the environment and the basic periodicity as due to the essential stability of the environment of animals of high biotic potential whose habits tend to insulate them from extreme climatic conditions.

Periodicity in Salmon Populations

A nine- to ten-year periodicity in the catch of Atlantic salmon was discovered almost simultaneously by Griswold (1929), Phelps and Belding (1931), and Huntsman (1931, 1937, 1938, 1941). Griswold's discovery was based on a study of the records of the Cascapedia and Restigouche Salmon Clubs and of the fishery statistics of New Brunswick and Quebec. Phelps and Belding corroborated Griswold's findings for the records of the Restigouche Club, finding a periodicity of nine or ten years extending back to 1879. Huntsman used the detailed fishery statistics of the Maritime Provinces which extend back to 1869.

Huntsman concluded that the periodicity in salmon was due to periodicity in rainfall. According to this explanation low water in streams caused by low rainfall exposes the large parr, on which kingfishers and mergansers feed, to increased destruction by these birds. Huntsman further argued that in addition to causing a lowered abundance of one year-class, low water favoured the survival of larger numbers of succeeding year-classes whose young are in the river at the same time, through decrease of cannibalism by the large parr on the younger and smaller salmon. Reduction of the numbers of fish-eating birds has been shown by White (1939) to have more than doubled the number of young Atlantic salmon surviving to the descending smolt stage. That destruction of fish predators increases the survival of young fish was also indicated by the experiments of Foerster and Ricker (1941). In an experiment extending over three years and involving the removal of an estimated 85 per cent of the squawfish, 40 per cent of the trout, and 60 per cent of the char, the rate of survival from egg to seaward migrant was increased three and a third times.

The conclusion that predators may sufficiently affect the size of populations as to bring about periodic fluctuations in fish is contrary to the generally accepted conclusions as to the effect of predators on periodicities among terrestrial animals. Errington in his exhaustive survey of predation and vertebrate populations (1946) concludes that there is more evidence of a significant effect of predators on fish populations than in the case of many other animals.

The four-year periodicity of the Fraser River sockeye salmon appears to be a characteristic of the population of that river system rather than of the sockeye salmon itself. No other sockeye population has a four-year cycle of abundance. The fact that the Fraser River sockeye is predominantly a four-year fish is probably in some way at the basis of its four-year periodicity in abundance. A large year-class once established tends to reproduce itself since the great majority of the Fraser River fish spawn in their fourth year. The Cultus Lake researches of Foerster (1938) under the Fisheries Research Board of Canada showed that the percentage of eggs producing seaward migrants was not much higher in small runs than it was in large ones. During three years (1925, 1927, 1930) of the Cultus Lake experiments comparing the relative efficiencies of natural and artificial propagation, the fish were allowed to reproduce naturally, and the results were as follows:

Year	*Number of adults*	*Per cent females*	*Eggs available for deposition*	*Seaward migrants*	*Percentages producing seaward migrants*
1925	5,423	73	17,470,000	197,700	1.13
1927	82,425	70	250,000,000	2,641,400	1.06
1930	10,395	53	24,900,000	804,300	3.23

The percentage of eggs producing seaward migrants was perhaps not significantly different when 250 million eggs were available for disposition and when the number was only seventeen million. Whether the discrepancy in the sex ratio is responsible for some of the variation in the success of reproduction cannot be decided on the basis of the experiments. It may be significant that the best reproduction resulted when the sexes were approximately equal.

Whether the big sockeye run in the Fraser every fourth year is due entirely to the reproduction of an exceptionally large year-class or whether the big run in some way interferes with the increase in population of the following three years is still a matter for speculation. The fact that in many other species of animals the attainment of dense populations makes the maintenance of such populations impossible suggests that the operation of the same principle be investigated in the case of the Fraser River sockeye.

Two possible ways in which a big year-class may interfere with the production of succeeding year-classes are, first, through older fish preying on younger ones and, second, through removal of some essential nutrient such as phosphorus from the water of the lake in which the young spend a year.

When the adults die after spawning, the disintegration of their bodies must add various nutrient materials, including phosphorus, to the lake through which they pass on their way to the tributary stream in which they spawn. Such nutrients support a growth of plankton which is eaten either directly or indirectly by the young sockeye during the year or more they spend in the lake. A large population of young might lock up in their bodies a considerable proportion of certain nutrients until they in turn die and disintegrate after spawning. Russell (1930 and other papers in the same series) found that a serious decline in the numbers of young fish in the English Channel was correlated with a marked change in the amount of phosphate in the waters. It therefore seems possible that the periodicity in sockeye abundance may be correlated with a periodicity in the supply of some element such as phosphorus which is locked up in the fish.

Another striking periodicity occurs in the case of the pink salmon (*Oncorhynchus gorbuscha*) whose spawning runs almost always occur only every other year. In northern British Columbia the runs are generally in the even-numbered years whereas farther south they are in the odd-numbered years. This species matures in its second year, so that fish which spawned in 1946 were the progeny of fish which spawned in 1944. The fact that runs usually occur only every other year means that there is only a single population which reproduces itself every other year. In explaining the two-year periodicity it is therefore necessary to look for an explanation of the absence of an entire year-class and its progeny through a long period of years.

Attempts of the Fisheries Research Board of Canada to establish a run in McClinton Creek, Queen Charlotte Islands, by transferring to it eggs and young derived from a population which occurred in another part of the islands in the off-years of the McClinton Creek run, failed. The attempts were repeated six times between 1930 and 1942. The reason for the failure of the eggs and young from another population planted in McClinton Creek to produce adults which returned to that creek was not discovered. By distinctively marking the young by the removal of certain fins it was known that none returned to the original stream from which the eggs were derived. Only a very few were taken in commercial fishing operations in spite of the fact that rewards were offered for information supported by the appropriate fin scars of adult fish taken in the fishery. Either the young failed to survive or the adults went to unfished parts of the ocean from which they failed to return to either the original or foster home streams.

The suggestion that a run of pink salmon in one year in some way interferes with the establishment of a population in the following year is strengthened by the fact that when efforts were made to establish pink salmon in some streams in Maine, the fish apparently survived only every other year (Huntsman and Dymond, 1940). Dr. Huntsman has suggested that one year-class eliminates the following one by preying on its young.

IMPORTANCE OF POPULATION STUDIES

Problems presented by fluctuations in animal populations are important for both practical and scientific reasons. In fisheries and wildlife management we are concerned basically with the size of populations. If a species is useful we are usually concerned with increasing its numbers; if it is destructive to our interests our problem is to reduce its numbers.

Before we reach the stage at which we can control an animal's numbers we may be able to predict the approximate size of its populations. Such ability is often of considerable economic value, for instance in planning for the handling of the expected crop in the fur trade or in fisheries. Also, in cases where control is impossible it will often be of economic value to understand the factors producing the result; for instance, the expenditure of funds to increase the population of an animal in a mistaken belief as to the cause of its scarcity may thus be prevented.

The application of a knowledge of cycles to conservation has been discussed by Butler (1942). He estimates that by appropriate conservation measures the fisher catch could be doubled, the lynx catch tripled, and the marten catch increased five times.

Elton on several occasions (1924, 1930, 1942) has emphasized the importance of periodic fluctuations in animal numbers in determining the course of evolution. When the population is at a maximum, selection takes place according to the ability to resist disease and to obtain mates and raise young successfully. At the minimum the animals are selected for their ability to avoid enemies, find mates, and resist unfavourable environmental conditions. Thus selection affects different attributes at the two stages of the population cycle. At the time of the increase in population a mutation having little or no adaptive significance may have an opportunity to become established since there is then relatively little struggle for existence. Elton has enlarged on this subject in a little book entitled *Animal Ecology and Evolution.*

Since epidemics of disease often result when animals reach high levels of population density, the relation of fluctuations in animal populations to public health must be considered. The fact that plague, tularaemia, typhus, relapsing fever, and several other diseases are associated with various rodents is sufficient to emphasize the importance of animal population studies to epidemiology. Cameron (1938) has also pointed out the relation of parasites of wild animals to the health of domestic animals. The comparatively recent discovery by Wells (1937) that a form of tuberculosis occurs in voles in England suggests the possibilities of research in this hitherto largely neglected field.

Many of the principles discovered in studies of the populations of the lower animals will also find application in human affairs. As Pearl (1937) repeatedly emphasized, the biological principles underlying population phenomena are fundamentally identical in man and in other animals. The logistic curve rediscovered by Pearl and Reed in 1920 (originally discovered by Verhulst (1839) nearly a century before) as a result of a study of the growth of the human population of the United States has been shown to apply to a wide range of lower organisms.

The fact that there is an optimum population for animals which is neither the maximum nor the minimum must be as true of human beings as it is of the other animals. One is tempted to speculate as to the possible similarity between certain characteristics observable among human populations today and the abnormal behaviour apparently produced among certain of the lower animals by crowding. Pearl, who had given so much thought to this subject, was inclined to believe that there were evidences of discomfort associated with the present density of human population and asked, "Can it be honestly denied that on a world-wide view, *unrest* is the dominant characteristic of human behavior today?" That was in 1937. He hoped that mankind might be able to evolve techniques of living happily and contentedly at high population densities in a physically limited universe.

Population Studies in Progress on Canadian Animals

Population studies in Canada to date have not been commensurate with either the need or the opportunity. In no country perhaps are fluctuations in animal populations more pronounced than in Canada. This is especially true in the case of fluctuations of a cyclic or periodic nature. These, of course, are characteristic of all northern areas but we are surely not going to be satisfied to wait for others to solve them for us. These periodic fluctuations present a special challenge to us for two reasons. One is because they are especially characteristic of Canada at least as far as the New World is concerned and the other is because they offer such opportunities for prediction of population trends.

Although population studies have been entirely inadequate in Canada, some useful work has been done and a number of projects have been started which, if properly supported and expanded, promise to yield valuable results in the future.

Some of the researches of the Fisheries Research Board of Canada concerned with populations have already been cited. Some others are as follows:

The Pacific Biological Station has for many years carried out a comprehensive programme of sampling the commercial catch of herrings and pilchards in waters off the British Columbia coast with the object of determining population trends with particular reference to size and age-class changes. Previous to the last herring fishing season the Station was able, as the result of the analysis of data based on a study of extensive samples, to predict the entrance of a rich year-class into the fishery in one of the fishing areas. Racial studies supported by tagging experiments had proved that there is comparatively little intermingling of herring constituting the populations of such fishing areas as the west coast of Vancouver Island, the east coast of Vancouver Island, a central area, and a northern area. It is therefore necessary in following population changes to sample the stock in each area separately.

In contrast to this condition in the herring of a number of rather discrete populations existing, there is free interchange in the case of another Pacific coast fish, the pilchard, between Canadian and Californian fishing grounds.

Most of the pilchard spawning takes place rather less than one hundred miles off shore between San Diego and Point Conception in southern California and north and south migrations satisfactorily explain the supply of pilchards to Canadian waters. Each succeeding summer as the young pilchards grow older they move farther north along the California coast returning southward again toward autumn. The larger fish go farther north and they take a longer time to get back. The largest fish usually appear off the British Columbia coast in summer, off San Francisco in early winter, and still farther south in midwinter.

Sampling and age determinations have shown that the pilchard supply is recruited by annual broods of widely varying strengths. The broods of 1939, 1938, and 1937 were strong or fairly strong but were succeeded by weak ones, which is the chief reason for the poor pilchard catch during the past year or two.

At the Atlantic Biological Station of the Fisheries Research Board, lobsters have been tagged so as to be recognizable until they moult. By determining the proportion which such tagged lobsters constitute of later catches not only is an estimate of actual population in an area obtained but also the rate of mortality due to fishing. By this means it has been determined that in twelve areas studied, from forty to eighty per cent of the market-size lobsters are caught during the fishing season.

Creel censuses in eight lakes in Charlotte County, New Brunswick, carried out over a period of years have shown that, in spite of stocking, the yield to anglers was on the average less than one pound per acre. Similar studies, although for shorter periods, on the same type of lake in other parts of New Brunswick and Nova Scotia have revealed yields usually of the same order. In contrast, two ponds in a more fertile region, Prince Edward Island, yielded respectively forty and ninety-two pounds of trout per acre.

Estimates of the population of smelts (*Osmerus mordax*) supporting the fishery in the estuary of the Miramichi River, New Brunswick, have also been attempted through the tagging and release in 1946 of 50,000 individuals. Only 0.36 per cent of over 500,000 smelts taken in the commercial fishery during the next ten days were found to bear tags. Examination of samples of smelts constituting the spawning run to brooks entering the main river and the north-east branch failed to reveal a single tagged fish entering these sections. This is interpreted as indicating that the population in the estuary towards the close of the fishing season probably represents the advance run of spawning fish which go farthest up the river to tributaries entering the south-west branch and that fish which spawn in tributaries of the main river and north-west branch enter the estuary after the close of fishing operations. These studies are only in their preliminary stages but they indicate the sort of information that may be derived from population studies of this kind.

The Ontario Fisheries Research Laboratory of the Department of Zoology, University of Toronto, in co-operation with the Ontario Department of Lands and Forests has carried out creel censuses on many of the lakes of Algonquin Park over a period of eleven years.

The character of the sockeye populations of several of the river systems of British Columbia has been recorded for thirty years. This study which was commenced by Dr. C. H. Gilbert in 1915 was continued for years by Dr. and Mrs. W. A. Clemens and more recently by Dr. Clemens (Clemens, 1945). Since for the solution of many population problems records over long periods are necessary, studies such as those on the sockeye salmon populations are especially valuable. It is to be hoped that records of this kind which have been in progress for so many years will not be allowed to lapse.

The Bureau of Animal Population, Oxford, with the co-operation of the Northwest Territories Administration, the National Parks Bureau of the Department of Mines and Natural Resources, and the Hudson's Bay Company is carrying out two questionnaire inquiries. One is entitled "Canadian Arctic Wild Life Enquiry." The results of this have been published annually in the *Journal of Animal Ecology* since 1938 (Chitty *et al.*, 1938-45). The results of the other, entitled "The Snowshoe Rabbit Enquiry," are being published in the *Canadian Field-Naturalist* (Elton *et al.*, 1933-43).

The Hudson's Bay Company, both independently and in co-operation with the Bureau of Animal Population at Oxford and the Royal Ontario Museum of Zoology, is contributing significantly to our knowledge of the populations of Canadian fur bearers. Since 1925 many of the Company's posts have furnished annual reports on fluctuations of wild life within their areas.

A questionnaire inquiry similar to that of the Bureau of Animal Population but with special reference to Ontario and including a wider range of birds and mammals has been carried out by the Royal Ontario Museum of Zoology since 1935. As Elton (1942) says: "The questionnaire system is still the only method which gives quickly and conveniently a general picture of fluctuations over vast areas."

A special feature of the Museum's questionnaire project since 1938 has been the accumulation of information on the periodic appearance of snowy owls in southern Canada and the northern United States. The Museum is headquarters of a co-operative programme for the compilation of data from Manitoba and Minnesota in the west to Washington, D.C., and Nova Scotia in the east (Snyder, 1943).

The Royal Ontario Museum of Zoology has also been carrying on annual censuses of small mammals in Algonquin Park since 1939.

Dr. W. Rowan of the University of Alberta has been actively interested in the problem of periodicities in hares, grouse, and other animals for many years and has accumulated a great deal of data on the subject, especially as it applies to Alberta.

Recommendations

The study of animal populations is of sufficient importance to Canada to warrant the establishment of an organization for the promotion of such studies. Such an organization should either be a research institution comparable with the Bureau of Animal Population at Oxford or a body charged with the responsibility of stimulating and co-ordinating work in this field by research institutions in various parts of the country. Present research agencies engaged in population studies need to be strengthened and much new work undertaken.

Extension and improvement of population studies should include:

1. Provision for better commercial fisheries and fur statistics. Regions for which statistics are separately recorded should be natural production units. When these have been established on a proper basis, records for them should be continuous and consistent.

2. The undertaking of studies designed to improve the accuracy of censusing various types of aquatic and terrestrial animals.

3. Plans for making and recording annual censuses over a long period of years of a number of important mammals, birds, fish, insects, and other animals.

4. Greatly increased provision for the study of the parasites and diseases of animals in nature since parasites and disease play such an important part in the fluctuations of animal numbers.

Few fields of research in Zoology offer better opportunities for making contributions of both practical and theoretical importance than does the field of animal populations and the factors affecting them.

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